# A Framework for Modeling Mosquito Vectors

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## Abstract

Vector-borne diseases account for 16% of the global infectious disease burden [26]. Many of these debilitating and sometimes fatal diseases are transmitted between human hosts by a mosquito. Mosquito-targeted intervention methods have controlled or eliminated mosquito-borne diseases from many regions of the world but holoendemic areas of transmission still exist [23]. These areas require a smarter and sharper system of intervention. To measure the impact of various intervention methods, there should to be a unified method for modeling mosquitoes in an agent-based simulation environment. This method should be flexible enough to model different species and genera of insects. In this paper, we propose a solution on how to model the life cycle of two genera of mosquitoes within a unified software architecture. The model's structure describes the gonotrophic cycle of the insects and the simulated phenomena are well documented in the biological literature. The reproduction of the biological phenomena contributes to the validation of our design and model.

## 1. INTRODUCTION

Vector-borne illnesses are transmitted between hosts by an intermediate organism. The primary vectors of debilitating diseases such as malaria, dengue fever, and lymphatic filariasis are mosquitoes. Vector-borne illnesses account for around 16% of the infectious disease burden globally [26]. Malaria is the most serious of these illnesses and is caused by a parasite that requires both a human and a mosquito host to complete its life cycle. More than 500 million people become ill with malaria every year with over a million deaths, mostly in children under five years of age [26]. Even vector-borne diseases that are not usually fatal, such as river blindness and lymphatic filariasis, can result in severe disabilities that limit the economic and social development of entire communities [17].

Malaria occurs throughout the tropics but particularly plagues sub-Saharan Africa, where it is considered a holoendemic disease. Many studies have focused on the mortality of the disease on populations under 5 years of age [9], [25], [14]. In Africa, malaria causes 18% of childhood deaths [5]. Eradication of diseases like malaria will save the lives of countless children throughout the world. These diseases have been removed from geographic areas before. The United Nations has been successful at local eradication by targeting the mosquito population. Despite these efforts, holoendemic areas of transmission require a sharper and smarter use of interventions [12] like bednets and drug administration. In order to maximize the effectiveness of intervention methods, their impact on a mosquito population can be evaluated through formal modeling and analysis. Models of malaria transmission have been used to predict the impact of disease interventions [22].

Breakthroughs are being made in modeling the transmission of these diseases, their active members and their dynamics [15], [3], [8], [19]. Among the various modeling techniques available, agent-based methods [21] show the most promise. In these models, each member of an interaction or system is treated as an individual with a set of rules dictating their behavior [21]. By observing the interaction between agents and probing the system at choice times, system-level properties can emerge providing insight into the engine of disease transmission [2]. This approach to modeling is conducive to evaluating the benefit of certain intervention methods and to anticipating possible behavior changes of the mosquitoes.

Modeling is rarely a trivial task and modeling a biological system can be very difficult. With every genus and species of insect, there is a whole new set of behaviors to characterize. Entomological simulations require millions of agents to accurately reflect the reality of holoendemic regions. The agent-based tools out today fail to address the complexities unique to this problem. Repast [7] and Swarm [18] do not ensure that the simulation's structure is optimally parallelizable. Neither allow for easy ways for an agent to pass between environments. In addition, there is not a specification for the interaction between agents and the environment. We are not proposing a replacement to these tools but an architecture that can be used concurrently with them.

We argue that there is a need for a unified architecture to model mosquitoes as separate agents. Such an architecture should have at least two forms of environments for the two stages of the mosquito's life cycle. Environments should be able to handle space, time, temperature, rainfall and other environmental variables while ensuring the effects of these variables are within a defined scope. There must be a transparent interface between mosquitoes, aquatic habitats and the environment. It must be extendable to different genera and species without much additional work. Finally it needs to be designed with the potential to simulate millions of agents simultane-

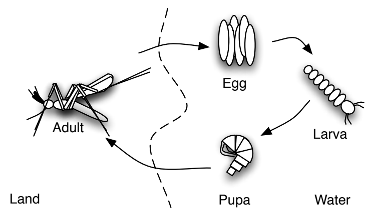


**Figure 1.** The life cycle of mosquitoes.

ously since mosquitoes exist in massive cohorts.

We describe such an architecture in this paper. It is capable of accurately encoding a mosquito's life cycle and behavior in a structure we call a strategy. The strategy is flexible and can be adapted to accurately characterize a new genus, species or variation within one species. The architecture is designed such that there can be an arbitrary number of nested subenviornements which the agents can interact with when egg-laying and when they are in the aquatic stage of their life cycle. Finally, the movement of agents between environments is handled through message passing making this system ideal for parallelization across many cores or many computers with existing tools like OpenMP [6] and MPI [13].

The following section describes the challenges in modeling mosquitoes. Section 3 will introduce a framework to deal with these challenges. Section 4 serves as a proof of concept that the framework is extendable. Section 5 concludes this work.

## 2. COMPLEXITY OF MOSQUITOES

The majority of species that act as vectors of human disease are flies (order *Diptera*), primarily mosquitoes (family *Culicidae*). Mosquitoes particularly are able to exploit resources quickly as they become available, have short generation times, and lay many eggs at once.

Mosquitoes spend the immature stages of their life in some sort of aquatic habitat and emerge as adults into the open-air environment (illustrated in Figure 1). A female mosquito lays a clutch of eggs in a pool or other collection of water. These eggs hatch and go through several stages of larval development before turning into a pupa and eventually emerging from that pupa as a fully formed adult. When mosquitoes emerge, they take some time to harden their exoskeleton and then seek a mate. Once mated, females of certain species need to take a bloodmeal in order to obtain the protein and nutrients required to develop a batch of eggs. The female seeks out a blood host, obtains a blood meal and takes some time to digest the blood and develop her batch of eggs. When the eggs are fully developed, the female seeks out a suitable aquatic habitat and lays her eggs on the surface. The length of time between consecutive bloodmeals is known as the gonotrophic cycle and is an important parameter in estimating the length of time between when a vector takes an infected blood meal and when it can transmit that disease.

This mosquito life cycle can be partitioned into basic aquatic and adult stages. The different stages of aquatic development can be simplified to the egg, larvae, and pupal states. The adult life stage can be subdivided into the different types of adult behavior. Though genera and species of mosquitoes might differ in the time spent in different stages, a flexible model that accounts for the basic biology of a vector would be applicable to many different types of disease vectors. For example, even non-mosquito vectors like sandflies, whose larvae develop in the soil, still have distinct immature and mature life stages and adult behavioral patterns that are common to blood-feeding insect [29]

Most models of malaria are based on the Ross-Macdonald model for disease transmission dynamics with a human host, a mosquito vector, and the malaria parasite. This model predicts that the mosquito survival rate is an important target for the control of malaria infection [20]. Classic malaria models are also based on the major African malaria vector species *Anopheles gambiae* and *Anopheles funestus* [3]. Malaria models are important for analyzing the potential impact of control efforts [4], but these models have rarely been applied to vector scenarios outside of the typical sub-saharan African transmission environment and often do not take into account the complex population dynamics of the mosquito population. In certain regions of the world, there may be more than five different mosquito vectors contributing to malaria transmission in a single area. It is important to be able to evaluate how these different species might contribute to disease and how they would interact within the same environment.

Changes in the density of a mosquito population and mosquito survivorship can be dramatically influenced by environmental variables such as temperature and precipitation. Shifts in temperature can influence the development time of immature stages, the flight activity and survival of adults [5]. Precipitation in a region determines the number and quality of breeding habitats available. Since many vector-borne diseases occur over a large geographical range, a model that allows for changes in environmental variables and accurately represents a vector population's response to those variables is critical for predicting disease risk. In a time when people are reconsidering the prospect of worldwide malaria eradication, it is increasingly important to examine many different transmission scenarios for the possibility of disease intervention [6].

## 3. MOSQUITO VECTOR MODELING

The previous section stated the needs of a simulation environment for modeling mosquito vectors. This complexity suggests an agent-based model with discrete time simulation. This will give each agent (mosquito) a set of states which characterize their biology and associated behaviors. We have

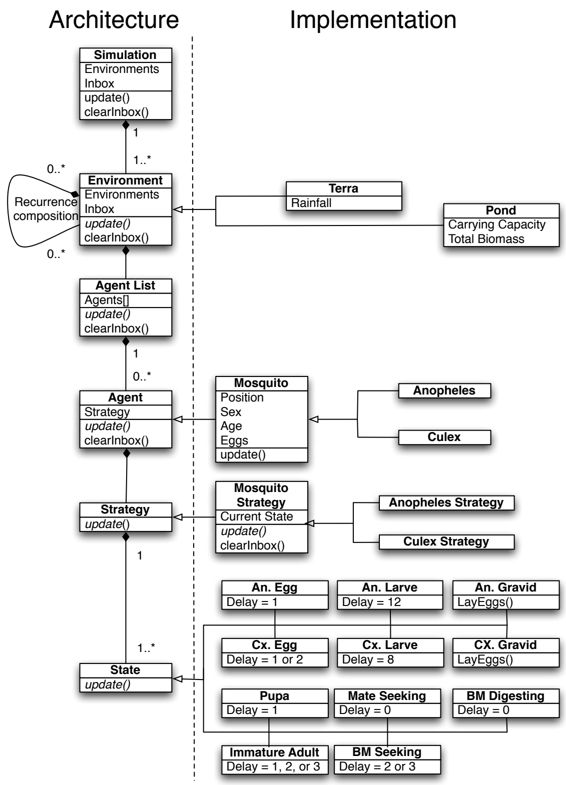


**Figure 2.** Class diagram of the simulation architecture. Left of the dashed line is the architecture; right of the line is the implementation described in this paper. Most of the classes in the left are abstract.

designed an agent-based modeling framework with the following specifications. There is a flexible time resolution for discrete events. Environments can contain subenviornments. Complex agent behavior is built using simple building blocks forming a coherent strategy. Non-mosquito agents are allowed and have their own strategy. Finally, our framework makes use of message passing and was structured to be parallelized.

## 3.1. Structure

Our framework defines six building blocks that make up the architecture. The structure of these components is displayed in Figure 2 and has a clear hierarchy. The remaining content in this section describes the responsibilities for each component in the framework. Each class is an abstraction allowing this model architecture to be extended beyond entomological applications despite the context of this paper. The following class descriptions will begin with the highest-level class and work downwards.

At the root of the hierarchy is the simulation. This object is responsible for maintaing time and other variables relevant to all environments. The simulation class also contains a listing of environments and an inbox. The inbox object will be described in the next section when the method for passing agents is discussed. It's the simulation's responsibility to be the heartbeat for the system.

Contained within the simulation is a set of discrete environments. Multiple environments provide a mechanism for the partitioning of the simulated world into manageable sections (both conceptually and pragmatically). Environments interface with their parent containers to access and inherit variables but can also contain their own local variables. Within an environment is a list of subenvironments which can be discrete elements (ponds, puddles, houses, etc) or territories. Another critical member of an environment is its agent list.

Agent lists are containers holding all the agents within an environment. An agent list for a given environment does not contain agents existing in subevironments. At their most simple, they are an array of agents but they can be reimplemented to perform population-wise functions. Agent lists can be easily extended to perform more advanced data-base style queries on the agent population within a given environment.

Agents are the autonomous beings which operate in a given environment. They consist of a set of variables describing their attributes. The behavior of an agent is affected by environmental variables and its own characteristics. The operations of an agent are encoded into a structure known as a strategy.

A strategy is an agent's brain. It's a state diagram (similar to a Moore machine) which governs how an agent interacts with other members of the simulation. The strategy preserves the states of an agent and how those states are arranged.

States are distinct elements describing an agent's action or inaction at any moment in time. States are connected to others through edges. States consist of an entry point, a time delay, behavioral decision rules and pathways to other states. The entry point sets initial conditions for the state. The time delay pauses the agent for a given period. This can be a relative time (1 hour) or an absolute time (3:05 P.M. or next Thursday). After the delay, behavioral decisions are made. The decision is an algorithm defined by the programmer which can take into account both environmental and agent-specific variables. The algorithm determines which state the agent moves to next. States can probe the environment through interfaces mimicking sensors or interact with the environment when moving or finding other agents or other environments.

## 3.2. Message-Passing

It is very common for an agent to move between environments in an entomological simulation. When an aquatic pupa emerges as a mosquito, it moves out of a pond and into a terra environment. When an agent flies across a spatial boundary between two environments, it passes from one to another.

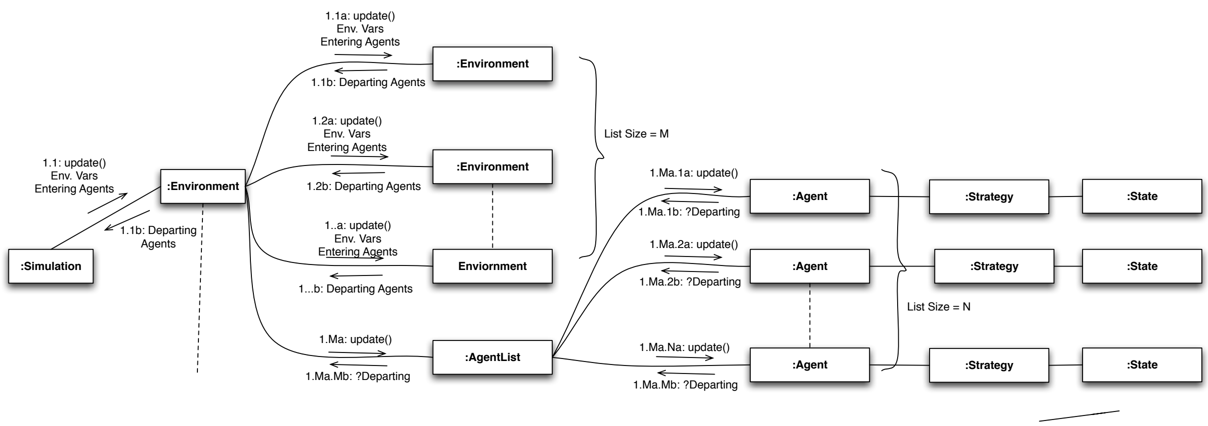


**Figure 3.** Communication diagram to illustrate the message passing during one simulation timestep.

This section describes how this movement is performed.

Every environment has knowledge about its parent container (the simulation or another environment) and its own subenvironments. When an agent's strategy decides the agent is to pass between environments, it addresses the agent to the appropriate environment and places it in the parent container's inbox. The address is a descriptor for the environment so it knows where to route the agent.

In an entomological simulation, there are three common ways for an agent to pass from one environment to another: injection, emergence and movement. Injection happens when an adult inserts an egg into a pond. In emergence, a pupa has matured into an adult and goes from a pond (subenvironment) to a terra (parent environment). Movement is the passing of an agent between two terras.

When a mosquito is laying eggs, new agents are created and injected into a pond (subenvironment). Programmatically, this is done by the mosquito strategy querying the terra for a pond. Eggs are created by the mosquito via the strategy and placed into the pond's inbox.

For emergence, the agent's strategy decides that it is time to transition from the pond to the terra. The strategy interfaces with the pond informing it of the change. The pond removes the agent from its agent list and places it into the terra's inbox through a message. The agent, strategy and all, is received by terra and waits in its inbox.

When an agent moves between terras, it is going between two environments of equal rank in the hierarchy. This is allowed in the simulation through implemented routing. The strategy detects the transition between two environments by checking the agent's position against the terra's bounds. The strategy informs its terra of this event. The terra removes that agent from itself and sends it to the parent object (the simulation). The agent waits for routing in the simulation's inbox.

Inboxes, seen in the class diagram, contain agents that are being inserted into an environment. For each agent in the inbox, the address is checked. Addresses are descriptions as to where the agent needs to go. If it is determined the containing object is the agent's new home, it is added to the environment's agent list. If it is determined that the agent is bound for a subenvironment in that object, it is added to that subenviornment's inbox and awaits processing.

Messages can be passed internally through shared memory or they can be sent between computers. Internal messages will allow for one simulation to be threaded in one machine using a tool like OpenMP. The simulation can be distributed over a cluster using MPI. These methods will allow simulations to take better advantage of multi-core machines and computing clusters.

## 3.3. Updates

An update refers to the refreshing of all the elements during one time step. Every element of the simulation has an update function and updates occur in a recursive fashion. The call traverses the hierarchy in a depth-first fashion.

The first update pulse is handled by the simulation. Upon receiving this instruction, the simulation updates all the independent, global variables and then clears its inbox. All the the agents within the simulation's inbox are routed to other environments. When the inbox is clear, the simulation calls the update function for each environment.

For all environments, updates happen in the following manner. First, the environmental variables are refreshed. Next the agents in its inbox are added to its agent list or routed to an appropriate subenviroment. Then the agent list is told to update.

The agent list updates by first performing any list-specific operations. Finally, the agents are iteratively updated. The agents tell their strategies to update which, in turn, tell their current state to do so. An update to an agent's state can either have the agent remain in that state if it is delayed or have the agent transfer to a new state.

### 3.4. Design Benefits

There are several major benefits to this design. First, agent behavior is easy to conceptualize and encode. Second, behavior is easy to alter and extend. Third, changes to objects in the simulation have a known scope. Forth, every agent sees the environment the same way. Finally, the method for transferring agents and for updating is conducive to parallelization.

This architecture presents a clear and concise method for encoding an agent's behavior. This is done by having a strategy consist of an implemented state diagram that interfaces with the agent and the environment. States within the strategy are responsible for one discrete action of the mosquito and it is easy to isolate and alter that behavior because of its narrow scope.

Every agent owns a unique version of its strategy. Therefore, it is trivial to add behavioral variation even within agents of the same species. Additional strategic complexity can be added without major revision to the simulation. Likewise, novel strategies can be easily created for new agent types.

The framework clearly defines the arrangement of objects and how those objects are updated. This ensures the program is broken into manageable bits whose scope is very well defined within the simulation as a whole. This is desirable as more complex scenarios are devised and experimental results hinge on how the changes made to the simulation propagate through to all the agents. Our framework guarantees that only changes visible to the agent effect the agent.

In the real world, all agents are working in parallel. This means that they are all sensing the same world at the same time. This idea is replicated in the simulation by locking the environmental variables before the agents are updated. This way all agents see the same snapshot of the world. Therefore, simulation results are not affected by the order in which agents are updated.

The hierarchical design, the message passing and updating processes make this system is easily parallelizable. Every environment on the same tier can be processed concurrently. Furthermore, the updating of all the agents within an environment can be threaded. Agents can move between environments either through shared memory or between machines through message passing. All communication is performed vertically and is designed so that deadlocks are impossible.

## 4. IMPLEMENTATION

The simulation framework was implemented in Java as seen in Figure 2 and 3. To prove our concept, we needed to implement at least two species that coexist in ecosystems. Of the 4500 mosquito species in the world, several hundred are capable of spreading disease. Two of the main groups of mosquitoes that carry disease are in the genera *Anopheles* and *Culex*. They have similar biologic life cycles but very different development rates and reproductive strategies. Since *Anopheles* and *Culex* coexist with different strategies, we chose them as agents in our simulation.

*Anopheles* mosquitoes are responsible for transmitting the malaria parasite *Plasmodium* along with certain filarial diseases. There are around 400 species of *Anopheles*, about 70 of which are capable of transmitting the malaria parasite [16]. These mosquitoes occur throughout the globe, mostly in the tropics. Due to their role in the transmission of malaria, *Anopheles* mosquitoes have been called the deadliest animal on earth.

Larval habitats of anophelines are usually small, semi-permanent pools of water, though some species have become specialized to breeding in more stable man-made habitats such as rice fields [24]. The length of *Anopheles* larval development is dependent on temperature and ranges from 8-30 days, with mortality increasing at the extremes of its temperature tolerance. *Anopheles* mosquitoes lay around 80 eggs per gonotrophic cycle. *Anopheles* mosquitoes have strong circadian rhythms and are generally active at night. Some species, like *Anopheles gambiae* and *An. funestus*, the primary vectors in sub-saharan Africa, have an extremely strong preference for human blood, which contributes to their ability to transmit malaria from person to person [10].

*Culex* mosquitoes are the primary vectors of the filarial worms that cause lymphatic filariasis. Lymphatic filariasis impacts 120 million people worldwide and, in its extreme form, manifests as the debilitating disease elephantiasis [17]. *Culex* mosquitoes, such as *Cx. quinquifasciatus*, also transmit many different human viruses, like West Nile Virus, St. Louis Encephalitis, Japanese Encephalitis, and others. *Culex* mosquitoes generally bite during the day so cannot necessarily be controlled using interventions like bednets.

*Culex* mosquitoes develop more quickly than anophelines and tend to lay more eggs. While anophelines may distribute their eggs in several different habitats, *Culex* mosquitoes lay their entire clutch of eggs at once, in a single habitat. Some species are capable of laying hundreds of eggs at once, but for the purposes of this model, we estimated that a female would lay several hundred eggs per clutch, much more than a typical anopheline would lay per egg cycle. *Culex* larval populations have density dependent mortality rates [27] [1], but may have a reduced sensitivity to crowding compared to anophelines [4]. Adult females have a 2-3 day gonotrophic cycle [11].

Because *Culex* mosquitoes have a shorter generation time and tend to lay more eggs than *Anopheles* mosquitoes, their populations react more quickly to environmental change, such as an increase in precipitation, and tend to quickly saturate the environment [10]. Adult mosquitoes of both groups adapt to sudden changes in temperature through behavioral modification. For example, at higher temperatures, adults can rest in cooler vegetation. Mosquito larvae usually respond to increases in temperature by increasing their rate of develop-

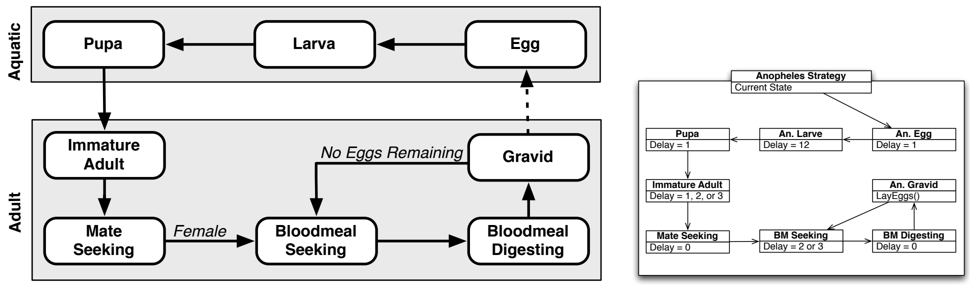


**Figure 4.** Mosquito life cycle represented as states (left) and its representation in *Strategy* (right).

| **Transition** | **Anopheles Gambiae** | **Culex** |
|---|---|---|
| *Egg* $\rightarrow$ *Larva* | 1 day | 1 (*p*=0.1) or 2 (*p*=0.8) days |
| *Larva* $\rightarrow$ *Pupa* | 10 days | 6 days |
| *Pupa* $\rightarrow$ *ImmatureAdult* | 1 day | same |
| *Immature Adult* $\rightarrow$ *Mate Seeking* | 1 (*p*=0.1), 2 (*p*=0.8), or 3 (*p*=0.1) days | same |
| *Mate Seeking* $\rightarrow$ *Mate Seeking* | immediate transition; males only | same |
| *Mate Seeking* $\rightarrow$ *Bloodmeal Seeking* | immediate transition; females only | same |
| *Bloodmeal Seeking* $\rightarrow$ *Bloodmeal Digesting* | 2 (*p*=0.7) or 3 (*p*=0.3) days | same |
| *Bloodmeal Digesting* $\rightarrow$ *Gravid* | immediate transition | same |
| *Gravid* $\rightarrow$ *Bloodmeal Seeking* | immediate transition egg count = 0 | same |

**Table 1.** Mosquito state transition times.

ment [28].

## 4.1. The Environments

We simulated an ecosystem where *Culex* and *Anopheles* coexisted in a terra and interacted with the same pond. The simulation had one terra containing all the adult agents.

The pond was a subenviornment to the terra and housed all the agents still in the aquatic state of their life cycle. The pond has two environmental variables: carrying capacity and current biomass. The carrying capacity refers to the amount of life a pond can sustain. The current biomass is the age-weighted sum of all the agents within a pond. The carrying capacity is increased with rainfall and available biomass was calculated with the following equation:

$$W = \sum_{Age=0}^{\infty} Age * Larvae_{Age}. \tag{1}$$

## 4.2. Agent Lists

Specialized agent lists were implemented to expedite population-wise operations. Mosquitoes die at age-specified death rates [30]. These rates were applied to the agents by cohort. The agent list was segregated into *Anopheles* and *Culex* types. Additionally, each type was binned by daily age. Death rates were applied by deleting the appropriate number of mosquitoes from each bin at random.

The age-specific mortality rate for adult mosquitoes was calculated using the following logistical form:

$$ASMR_{Age(adult)} = \frac{\alpha * e^{\frac{Age}{\beta}}}{1 + \alpha * s * \beta(\alpha * e^{\frac{Age}{\beta}} - 1)} \tag{2}$$

where $\alpha$ is set to the baseline daily mortality rate, $\beta$ and $s$ are constants defining the rate of increase and asymptote respectively. The base death rate, $\alpha$, was 0.1 for *Anopheles* and 0.3 for *Culex*. This equation was determined through experiments on mosquito aging [30].

Larval age-specific mortality rates were applied in the same manner as the adult mortality. Death rate was calculated by

$$ASMR_{Age(larvae)} = \alpha * e^{\frac{W}{Age*C}} \tag{3}$$

where C is the carrying capacity of the pond and W is the age-weighted number of larvae in the pond at the beginning of the day. Eggs and pupae were killed at a fixed mortality rate.

## 4.3. The Mosquitoes

*Anopheles* and *Culex* were easily implemented by subclassing *Agent*, *Strategy* and *State* and adding functionality specific to each genus. Both of these vectors are mosquitoes and follow the same basic life cycle illustrated in Figure 4.

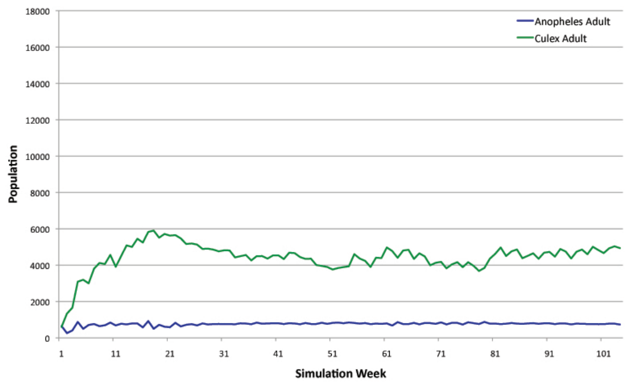


**Figure 5.** Anopheles and Culex adult populations without rainfall.

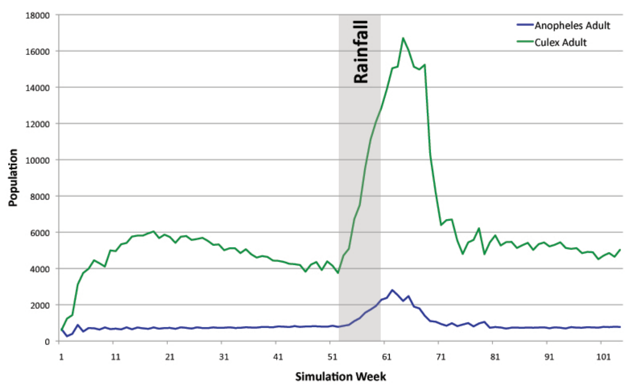


**Figure 6.** Results from the simulation with rainfall.

The state transition rules differ between the two forms of agents. The biologic differences are provided in Table 1.

*Culex* develops faster in aquatic habitats so their time in the pond is less than Anopheles (8 or 9 days compared with 12). There is a higher mortality rate for younger larvae in dense aquatic habitats because of resource competition and predation. *Culex's* strategy is to offset this high mortality by placing all of its eggs into a pond at one time. *Anopheles*, however, waits to lay eggs until an aquatic habitat has the capacity to sustain its progeny. Therefore, she commonly lays a small amount of her batch in many different ponds.

These biological difference were implemented by making trivial changes to the states of each agent. While digesting a bloodmeal, *Culex* produces 300 eggs in her clutch whereas *Anopheles* produces only 80. When deciding to lay eggs in the gravid state, Anopheles would deposit as many eggs as she sensed the pond could accommodate. *Culex* would lay all of her eggs into the pond.

## 4.4. Validation

We demonstrate this architecture can be used to model complex biologic systems by replicating a phenomenon seen in nature. The carrying capacity of ponds increase during the rainy season. This, in turn, increases the availability of oviposition sites. For example, a small pond can increase in size to a large lake. It is documented that this causes an increase in abundance of mosquitoes [23]. During this time, the *Culex* population grows at a much higher rate than *Anopheles* [28].

This trend can be simulated through the implementation we describe here by adding rainfall as an environmental variable at the terra level. We assume a constant rainfall over a 60 day rainy season. For each day of rainfall, the pond's carrying capacity increased by 500 units. For 60 days after the rain, carry capacity was reduced at a rate of 500 units per day. We ran one simulation where rainfall was not taken into consideration to gather an estimate of the baseline populations. The result for the rainless simulation is shown in Figure 5. The simulation with rainfall is shown in Figure 6. Rain was initiated at week 52 to give the system time to reach steady state.

The simulation results replicate what was found in [28]. There is an increase in both populations caused by the rainfall. The increase in *Culex*, however, is drastically higher than *Anopheles*. Each genus coexisted through the domain of the simulation.

# 5. CONCLUSIONS

This paper presented a framework for modeling mosquito vectors. Simulations are constructed using six building blocks arranged in a hierarchy. Mosquito biology and associated behavior is encoded into a structure known as a strategy. Strategies are composites of fundamentally simple states. Strategies are easily extended allowing for variation and complexity. Structure and order is maintained by giving every object its own specific and finite scope. Every agent has the same view so the order in which agents are processed does not matter. The framework has built-in mechanisms for message passing allowing for the framework to be parallelized. Though this framework has mechanisms for message passing, distributed simulation was not taken advantage in this work.

As a simple proof of concept, we implemented two genera of mosquitoes. *Anopheles* and *Culex* coexisted in a simulation during a rainy season. Biological studies demonstrate that rain affects both populations but *Culex* mosquitoes are more responsive. This phenomenon was replicated by our implementation. This demonstrated that our framework made simulations easy to build and extend (requiring less than 30 lines of new Java code).

# 6. ACKNOWLEDGEMENTS

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